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The Reinforcing Efficacy of Wheel Running as a Function of Deprivation for Food

by

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A THESIS

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled The Reinforcing Efficacy of Wheel Running as a Function of Deprivation for Food submitted by Douglas Peter Boer in partial fulfilment of the requirements for the degree of Master of Science.

Dedication

To my constantly supportive and caring parents, John and Coba Boer; and to the memory of Jeanne Hrynyk.

Abstract

The traditional interpretation of increase in activity by rodents during food deprivation is that of a motivational "link" between these events. However, from an operant perspective, the findings of the activity-deprivation literature are unusual. That is, these studies suggest that the reinforcing efficacy of wheel running is under the control of deprivation for food, a different stimulus. Thus, it is implied that wheel running should support more operant behavior under food deprivation conditions than during maintenance on free food. The present study was designed to investigate this assumption. The results of certain measures (postreinforcement pause, interreinforcement interval, amount of turns) were variable. However, data indicate that rats will consistently emit more bar-presses when food deprived than when maintained on *ad libitum* food to obtain one minute of free wheel time as reinforcement. The data also revealed that an inverted U-shaped function described the relationship obtained between the reinforcing value of wheel running and food deprivation. Theoretical implications of this relationship are discussed.

Acknowledgments

Although this thesis is not of Proustian proportions, many people have helped in various ways to make it part of my "remembrance of things past". First, tne time and effort invested in reading and constructively criticizing this paper by Dr. Frank Epling, who also acted as supervisor for the project, and also Dr. David Pierce and Dr. B. Sinha is gratefully acknowledged.

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In addition, many thanks go out to my family whose support and encouragement remain a constant source of amazement and "motivation" for me. Also, much of the credit for the completion of this "tome" belongs to my closest friend, Nicola, to whom I am indebted for changing the task of writing the thesis from a possibly arduous task to the very best of times.

Finally, a postscript to my relatives in Holland who have taught me to live by the creed, "'s morgens voor de koffie niet zeuren".

Table of Contents

List of Tables

List of Figures

I. INTRODUCTION

Within the experimental analysis of behavior, the principle of deprivation states that withholding a stimulus increases the reinforcing efficacy of that stimulus. That is, reinforcement value varies as a function of stimulus deprivation (Skinner, 1938). In contrast to the functional analysis of deprivation, the activity-deprivation literature suggests an alternative view of deprivation. Many studies have shown that certain species of rodents will increase activity as measured by wheel running when they are food deprived (e.g., Finger, 1951). Also, certain studies have indicated that wheel running is a high rate behavior, and as such can used as reinforcement for low rate behaviors such as bar-pressing (e.g., Kagan and Berkun, 1954; Premack, 1962). Hence, we can view wheel running as a reinforcing stimulus. By implication, these studies taken together suggest that the reinforcing strength of one stimulus may be shown to be under the control of deprivation for a <u>different</u> stimulus.

The operant view of motivation is based upon the operation of deprivation. Deprivation involves withholding a stimulus for a period of time, thus establishing a specific level of deprivation measured in terms of percentage free-feeding weight. Level of deprivation in turn increases operant behavior supported by that reinforcer. For example, Clark (1958) has shown that if a rat is deprived of food it will increase response rate on variable interval (VI)

schedules over that obtained when maintained on ad libitum food. The higher VI response rate sustained may be thought of as being representative of food having greater reinforcing "value" during deprivation. Thus, by this analysis it is implied that deprivation operations only affect behavior related to the deprived stimulus.

Recently, Premack (1962, 1965, 1971) proposed a model of the relative nature of reinforcement. According to Premack's formulation, reinforcement may be measured as relative frequencies of behaviors which organisms can engage in. That is, for any two given operants, if the higher frequency operant is made contingent on the lower frequency operant, then the low frequency response will increase. Thus, the less frequent response may be reinforced by the opportunity to perform the more frequent response. Premack also claimed that the reinforcing "value" of a stimulus is indexed by the probability of an organism responding to that stimulus during an experimental session. [1] For instance, Premack (1962) established a contingency between running in an activity wheel and opportunity to drink. In this condition, rats which had restricted access to water, increased their frequency of wheel turning in order to obtain water. Premack later reversed these conditions, making the opportunity to run in the wheel contingent upon

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[1] According to Premack (1971), the "value" of a particular response is measurable by the momentary probability that an organism will engage in that response and the value of a particular stimulus can be measured by the momentary probability that the organism will respond to that stimulus at any time during an experimental session.

drinking. He found that rats greatly increased their amount of drinking in order to run on the wheel. Thus, he was able to show that running could be used to reinforce drinking and drinking reinforce running. Essentially, these results indicate that the reinforcing value of either operant was dependent upon deprivation for that activity. Important to the present study is the observation that wheel running behavior would support another operant.

Many studies have demonstrated that certain species of rodents will substantially increase activity as measured by wheel running when they are food deprived (Duda and Bolles, 1963; Cornish and Mrosovsky, 1965; Routtenberg, 1968; Finger, 1965). For example, Finger (1951) used rats at two levels of food deprivation, 24 and 72 hours, and found that the amount of running wheel activity increased markedly with deprivation level. In this respect, Premack and Premack (1963) determined that the increase in running during food deprivation is due to being deprived of a behavior (eating) recurrently comprising about 17% of a rat's total daily activity. These authors suggest that food deprivation as "activity deprivation" will lead to an increase in some other behavior such as running. Other studies have shown that wheel running is a high frequency behavior which can be used to reinforce instrumental behavior such as bar-pressing or tube-licking (Kagan and Berkun, 1954; Premack, 1962), revealing that wheel running can act as a reinforcing event. On the basis of the above studies and Premack's (1965) model

of the relative nature of reinforcement an important implication is suggested. That is, wheel running as a reinforcing event should support more operant behavior (e.g., bar-pressing) under conditions of food deprivation than under free food conditions. The present research was designed to investigate this possibility.

One possibility is that specific motivational operations may enhance the reinforcing efficacy of certain stimuli (cf., Clayton, 1958; Davis, 1958). For example, Clayton (1958) using rats found that deprivation for water increased the reinforcing value of light reinforcement. In a similar study, Davis (1958) using rats found that deprivation for food also increased the reinforcing strength of light reinforcement. These studies concluded that light presentation was more effective as a reinforcer for bar-pressing when an organism is water or food deprived than when not deprived. In both of these studies the animals used were exposed to an experimental period in which light presentation signalled the eventual presentation of the deprived stimulus. For example, in Davis' (1958) study certain subjects were deprived of food for 23.5 hours prior to a session and were fed immediately following the session. Davis found that these rats would significantly increase amount of bar-pressing over experimental sessions as compared to non-deprived controls. It was concluded that this increase was due to light reinforcement. Despite methodological shortcomings which question the validity of

this conclusion, these studies do suggest that it is possible that specific motivational relationships are typical for certain stimuli and behaviors.

Alternatively, it has been suggested that the increase in activity observed in food deprived organisms is due to a motivational "link" between these systems (Bolles, 1967). In this respect, certain studies which have found an increase in activity as a function of deprivation claim that such results support the notion that "drive" for a deprived stimulus exerts a directly "energizing" effect upon general activity (as measured by wheel running or various other activities such as bar-pressing, etc.) (e.g., Wright, Gescheider and Johnson, 1966). Whether a general "link" exists between food and activity, or only specific reinforcement relationships is not clear, although it is possible that this question may be tested. In either case, the activity-deprivation literature has determined that food deprivation increases activity. Thus suggesting that activity becomes more reinforcing with food deprivation level.

In summary, if the reinforcing efficacy of wheel running is dependent upon deprivation operations, changes in level of deprivation should correlate with similar changes in the reinforcing value of wheel running. Such changes in the reinforcing value of wheel running may be indicated by the "strength" of operant behavior indexed by changes in postreinforcement pause (PRP), interreinforcment interval

(IRI), number of bar presses sustained, and number of wheel turns consumed per opportunity (i.e., consumption of the reinforcer). Of primary importance, changes in the strength of a conditioned operant, such as bar-pressing on an increasing fixed-ratio (FR) schedule to run on a wheel under different levels of food deprivation, may be thought of as establishing a relationship between deprivation and the reinforcing efficacy of wheel running. Bar-pressing measures on a FR schedule were obtained instead of examining response rates on a variable-interval schedule since the former measure is a better reflection of the strength of the reinforcer in supporting behavior. The present study was designed to investigate this relationship in terms of the above variables.

II. METHOD

A. Subjects

4 male and 4 female 21 day old Sprague-Dawley rats were obtained from the University of Alberta Animal Colony (Ellerslie Animal Farm, University of Alberta). Prior to experimental procedures the animals were individually housed and were maintained on *ad libitum* food and water.

B. Apparatus

A standard Wahmann activity wheel was modified so that a solenoid-operated brake could be turned on or off. A retractable Leigh-Valley lever was adapted to fit the wheel entrance. Coulbourne Instruments solid-state equipment operated the brake and powered the lever. Data were recorded on a Coulbourne Instruments multi-channel print out counter. The modified Wahmann wheel was in a separate experimental room (continuous light, temperature of 20 $\pm$ 2 degrees Celsius) and the Coulbourne Instruments equipment and print out counter were in an immediately adjoining room.

C. Procedure

In the room where the rats were housed room lighting was provided on a 24 hour basis, and a temperature of 20 $\pm$ 2 degrees Celsius was maintained. The animals were brought in one week ahead of bar-press training to allow daily monitoring of weight, food-intake, and water-intake. This

allowed the rats to become adjusted to continuous lighting. All animals were initially trained to press the lever and then placed in the experiment at approximately 50 days old.

At the beginning of the training phase, all rats were exposed to 60 seconds of free-wheel and tone (60 Hz.) followed by 60 seconds of locked-wheel and no tone. This procedure continued until running occurred reliably in the presence of the tone. Following this, the retractable lever was extended into the wheel drum and a single bar-press was required to retract the lever, turn on the tone, and free the wheel for 60 seconds. Subsequently, the animals were shaped over a varying number of sessions to press the lever 20 times to obtain 60 seconds of free-wheel and tone (FR 20). Following the shaping procedure, subjects 3, 4, 6, and 7 were reduced over 16 days to 75% body weight by decreasing their daily food ration. During this time, subjects 1, 2, 5, and 8 were maintained at *ad libitum* weight. The animals did not receive exposure to a running wheel during this 16 day period.

When the deprived subjects (Ss 3, 4, 6, and 7) met criterion weight, all animals were required to press the lever on incrementing FR values for 60 seconds of free-wheel and tone. The FR requirement began at FR 5, and after three successful completions of this ratio, the requirement was increased by 5 to FR 10. After three successful completions of FR 10 the ratio requirement was again increased by 5 to FR 15, and so on. This procedure was continued until one

hour had elapsed without the subject completing a ratio requirement or until the session length exceeded 8 hours. Following this, free-food subjects were reduced over 16 days to 75% body weight while deprived subjects were returned to free-food conditions. Importantly, deprivation for the running wheel was held constant while deprivation for food varied across subjects. After the 16 day period, the animals were again exposed to the incrementing FR procedure at their new levels of food deprivation.

Following this phase of the experiment, subjects were exposed to the following body weight deprivation values (with at least a 16 day period between each value) in the order given for each animal. Rat 1 was tested at the additional points: 70% and 85%; Rat 2 at 85% and 70%; Rat 3 at 70%, 85%, and 65%; Rat 4 at 85% and 92.5%; Rat 5 at 85% and 70%; Rat 6 at 70% and 85%; Rat 7 at 85%, 70%, and 65%; and Rat 8 at 70%, 85%, and 65%.

The "reinforcing value" of wheel running was measured by the highest FR obtained, as well as the total number of bar-presses emitted per session, at each level of deprivation. That is, the largest FR value obtained, or the total number of bar-presses emitted per session, represents the amount of operant behavior (in this case, pressing a lever) supported by wheel running. In addition, data were obtained for PRP, IRI, and number of wheel turns consumed per opportunity.

III. RESULTS

The reinforcing efficacy of wheel running was expected to be greatest under conditions of food deprivation. Such increases in reinforcing value should be indicated by shorter PRP's, IRI's and a larger number of wheel turns consumed per opportunity. Table 1 presents these measures when calculated on equivalent FR values for each subject. Animals generally obtained larger FR values under deprivation conditions. Therefore, the data for each subject were averaged over the highest FR value common to all the deprivation conditions to which the animal was exposed (see Table 2). For example, in case of Subject 1 the data for all values up to and including FR 65 were summed and means calculated for each of the four body weight conditions used.

Although PRP, IRI and wheel turns emitted per opportunity do not systematically vary with deprivation conditions for all subjects, there were some regularities obtained. For instance, PRP varied systematically with deprivation for Subjects 1, 4 and 5. That is, greater PRP values were obtained at the highest and lowest deprivation points for each animal (i.e., 70% and 100%), with generally lower PRP values characteristic of the intermediate deprivation points (i.e., 85% and 75%). Thus, a U-shaped function describes these results. However, PRP measures for the other five subjects do not reveal such a consistent relationship between deprivation points and length of PRP. None the less, the PRP value obtained at the 100% end point

was greater than at least one of the other deprivation points for all subjects. The only exception to this was Subject 8 which exhibited no consistent changes in PRP by condition.

The IRI data was found to vary systematically with deprivation for Subjects 2, 3 and 4 obtaining a U-shaped function similar to that obtained for Subjects 1, 4 and 5 with regard to the PRP data. The IRI measures for the other five subjects do not indicate such a consistent relationship between deprivation conditions and length of IRI. Although, in general, like the PRP data, the IRI value attained under free-food conditions was greater than at least one of the other deprivation points for most of the subjects. The exception to this was Subject 8 which showed no consistent changes in IRI by condition and Subject 5 which demonstrated a lower IRI value in the 100% condition than under any other deprivation point.

Data reflecting number of wheel turns emitted per opportunity are related to deprivation conditions in a fashion similar to that of the PRP and IRI results. All subjects, except Subject 1, showed fewer wheel turns per opportunity at the 100% point than under at least one of the other deprivation points. For example, Subjects 6 and 7 generated fewer wheel turns under free-food conditions than during any other deprivation condition. Subjects 3 and 8 demonstrated fewer wheel turns under the 85% condition than the 100% condition, but attained greater values of wheel

turns at all other deprivation points. Subject 1 was an exception to the general findings and revealed greater wheel turn values in the free-food condition than under all other levels of deprivation. An interesting general finding was that over all deprivation conditions the female subjects (Ss 1, 2, 3 and 4) exhibited greater wheel turn values than did the male subjects (Ss 5, 6, 7 and 8). This result is probably not due to order of presentation of deprivation condition, because of the balanced nature of the design. However, it could be due to the large discrepancy in body weight between male and female subjects (see Table 3). Finally, wheel turns emitted per opportunity are systematically related to deprivation conditions in Subjects 3, 5 and 6 where an inverted U-shaped function could be used to depict these data.

The reinforcing efficacy of wheel running was expected to be indicated by the highest FR value obtained, as well as the total number of bar-presses emitted per test session. As can be seen from the results of Subject 5 the highest FR value attained at the 75% and 85% deprivation points are equal (i.e., FR 50). However, the absolute number of bar-presses emitted at these two points are different (i.e., 776 bar-presses at 85% and 748 at 75%). Therefore, it was decided to use total number of bar-presses to index reinforcement value of wheel running since the FR size variable was not sensitive to small changes in the independent variable (i.e., food deprivation). Figure 1

depicts the absolute number of bar-presses emitted per test session across all levels of deprivation. Female subjects are presented on one graph and male subjects on the other. In general, females emitted far greater numbers of bar-presses per session at all food deprivation conditions when compared to males. The only exceptions to this general observation are Subject 3 in the 100% conditions and Subject 4 in the 75% condition. This observation may be due to discrepancies in body weight between the male and female subjects at the various deprivation points, as males generally were heavier than females (see Table 3).

An inspection of Figure 1 reveals that an inverted U-shaped function was obtained for all animals. This function is more pronounced in the female subjects. The results of Subject 8 deviate slightly from the consistent inverted U function obtained for all the other subjects in that this rat obtained a lower total number of bar-presses at the 85% point than at the free-food end point. Subjects 3, 7 and 8 were exposed to 65% deprivation after the four main test conditions (see Table 3 for order of presentation of test conditions). Subject 4 was not exposed to the 70% deprivation condition since it was judged to be physically too weak to be deprived below the 75% level. Therefore, it was decided to test this animal at 92.5% deprivation, the midpoint between the 100% and 85% conditions to obtain a fourth data point. Interestingly, although judged to be too weak to be deprived past 75%, this subject attained its

highest mean wheel revolutions per opportunity during the 75% condition. This observation argues against the notion that the decrease in bar-pressing was due to starvation or deterioration of the physical condition of the animal.

There is a reliable drop in bar-presses sustained prior to, or at, the highest deprivation point for seven of the eight subjects. Subject 8 also revealed a drop in bar-presses at the highest deprivation point, but this drop is of a small magnitude in comparison to the other animals. Subjects 1, 2, 3, 7, and 8 produced this drop at the highest deprivation point whereas Subjects 4, 5 and 6 revealed this drop prior to the highest end point, showing an even more dramatic decrease in bar-pressing at the highest deprivation level (e.g., see Figure 1, Subject 4). The initial decrease in behavior occurs at 65% for Subjects 3, 7 and 8, at 70% for Subjects 1 and 2, at 75% for Subjects 5 and 6, and finally at 85% for Subject 4. In addition, a comparison of the 100% end points and the point prior to where the decrease in behavior occurs for each subject (i.e., 65%, 70%, 75% or 85% and 100%) shows that for all subjects except Subject 1 more behavior was emitted at this deprivation point than at the 100% point. This interesting observation tends to argue against the position that the decrease in behavior was due to physiological or physical breakdown of the animal. Finally, further support for this claim is revealed when the 100% end point and the highest deprivation point are examined. That is, five of the eight subjects

emitted more behavior at the highest deprivation point than at the 100% end point.

In conclusion, bar-pressing data demonstrate that the reinforcing value of wheel running varies systematically as a function of level of food deprivation. Interestingly, when wheel turns consumed and bar-pressing data are compared it does not appear that amount of turns per opportunity reflects reinforcing value of wheel running. The form of the function relating the reinforcing efficacy of wheel running (as represented by total number of bar-presses emitted per session) and level of food deprivation was an inverted U which was obtained for all animals. Such a reliable functional relationship was not found for the other measures of reinforcing value (i.e., PRP, IRI) for all subjects, but overall, these measures did suggest that food deprivation affects the reinforcing efficacy of wheel running. The bar-press data are of primary importance because of their consistent and systematic nature. Whereas the other measures (PRP, IRI, and wheel turns data) are of secondary importance as they lack a similar functional relationship with deprivation.

TABLE 1

Mean Post-Reinforcement Pause (PRP), Inter-Reinforcement Interval (IRI) and Wheel Revolutions (WHL) as a function of deprivation for food.[1] (Dependent Measure = DM; Subject = S)

		Percent Body Weight					
S	DM	100	92.5	85	75	70	65
1		86.2	-----	54.5	51.6	89.2	-----
2		54.2	-----	66.6	46.0	59.1	-----
3		119.6	-----	56.4	115.1	138.4	99.7
4	PRP	185.2	103.9	108.6	229.0	-----	-----
5		69.0	-----	67.4	56.7	60.8	-----
6		229.3	-----	161.9	154.3	117.4	-----
7		200.9	-----	425.3	227.7	208.3	101.2
8		100.9	-----	200.8	260.8	105.0	210.6
1		440.7	-----	545.7	319.9	679.7	-----
2		546.6	-----	382.5	319.5	440.3	-----
3		592.1	-----	345.9	412.9	354.5	558.4
4	IRI	327.2	197.1	302.9	828.8	-----	-----
5		441.5	-----	663.5	509.7	525.6	-----
6		434.5	-----	461.3	413.8	710.8	-----
7		449.9	-----	691.7	505.4	423.4	211.3
8		250.8	-----	435.5	489.9	311.7	476.4
1		39.0	-----	24.3	35.4	20.4	-----
2		30.0	-----	23.5	32.1	26.5	-----
3		17.4	-----	14.5	25.7	21.6	18.2
4	WHL	19.2	12.0	17.7	29.8	-----	-----
5		17.9	-----	22.6	17.7	13.7	-----
6		8.8	-----	12.4	21.3	16.7	-----
7		8.5	-----	14.1	17.8	16.9	17.5
8		9.5	-----	9.1	15.8	12.6	18.6

[1]Means are calculated on equivalent FR values since animals generally obtained higher ratios under deprivation conditions.

TABLE 2

Highest FR value obtained (FR) and total number of bar-presses emitted (TOTAL) per session as a function of deprivation for food. (Dependent Measure=DM; Subject=S)

		Percent Body Weight					
S	DM	100	92.5	85	75	70	65
1		70.0	-----	70.0	85.0	65.0	-----
2		75.0	-----	85.0	95.0	90.0	-----
3		40.0	-----	55.0	60.0	70.0	50.0
4	FR	45.0	60.0	50.0	25.0	-----	-----
5		45.0	-----	50.0	50.0	40.0	-----
6		35.0	-----	50.0	45.0	40.0	-----
7		25.0	-----	30.0	35.0	50.0	35.0
8		30.0	-----	20.0	35.0	50.0	50.0
1		1507.0	-----	1584.0	2125.0	1300.0	-----
2		1725.0	-----	2206.0	2870.0	2485.0	-----
3		565.0	-----	982.0	1203.0	1439.0	781.0
4	TOTAL	678.0	1234.0	854.0	240.0	-----	-----
5		660.0	-----	776.0	748.0	508.0	-----
6		379.0	-----	784.0	639.0	512.0	-----
7		246.0	-----	315.0	400.0	725.0	431.0
8		277.0	-----	171.0	437.0	762.0	728.0

TABLE 3

Weight prior to experimental session and order of presentation of each weight condition ( ) for each subject.

Subject	Percent Body Weight					
	100	92.5	85	75	70	65
1	238.2(1)	--------	214.9(4)	176.4(2)	165.9(3)	--------
2	218.0(1)	--------	182.7(3)	162.0(2)	159.8(4)	--------
3	256.3(2)	--------	212.1(4)	181.6(1)	173.1(3)	160.9(5)
4	249.1(2)	230.1(4)	212.3(3)	164.2(1)	--------	--------
5	307.8(1)	--------	256.9(3)	226.6(2)	210.2(4)	--------
6	350.7(2)	--------	291.9(4)	170.4(1)	237.7(3)	--------
7	362.5(2)	--------	305.0(3)	193.1(1)	250.4(4)	231.8(5)
8	328.9(1)	--------	273.4(4)	239.7(2)	224.8(3)	208.0(5)

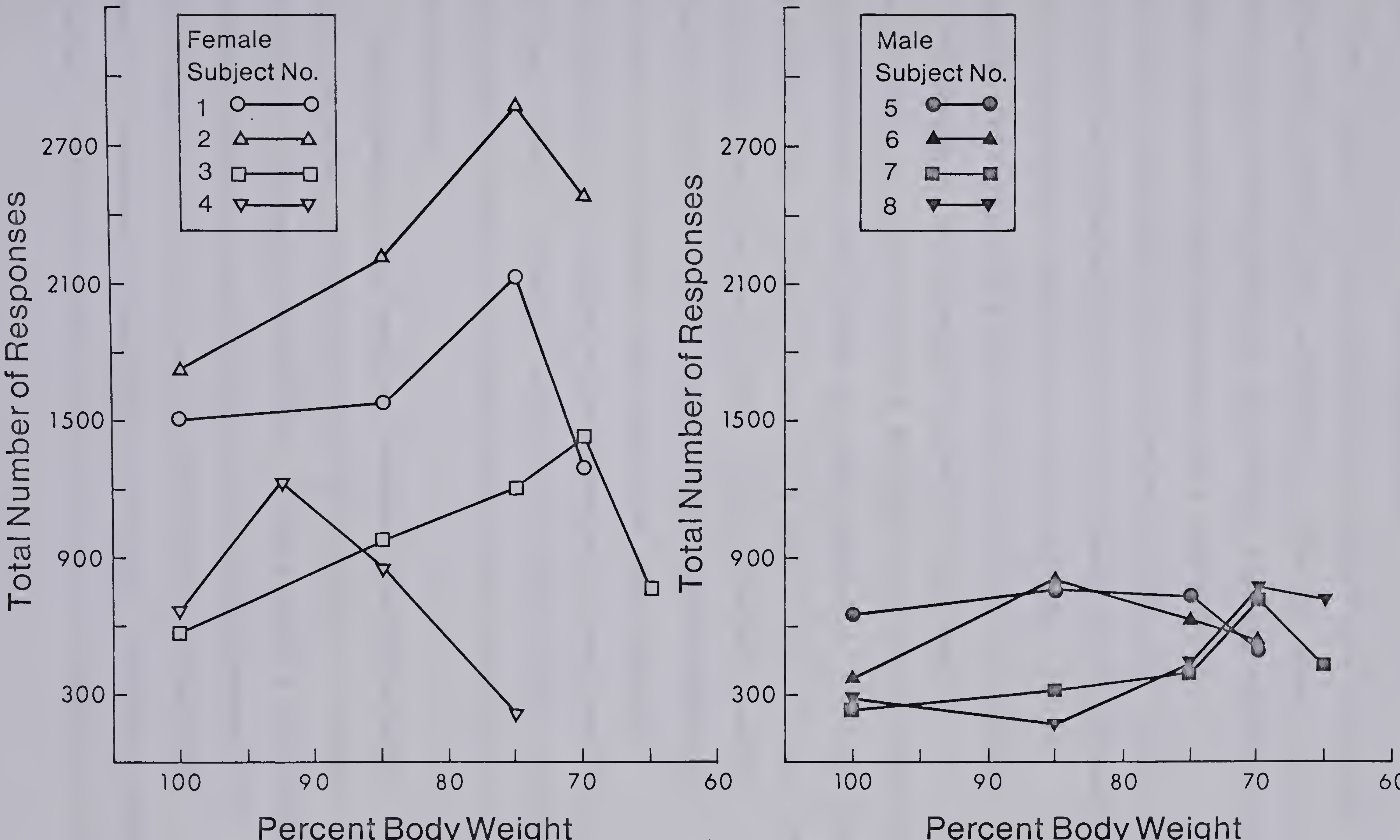

FIGURE 1: Total number of bar-presses emitted as a function of deprivation for food.

IV. DISCUSSION

The results of this experiment demonstrate that food deprivation affects the reinforcing value of wheel running. Specifically, data indicate that wheel running sustains more operant behavior (bar-pressing) as a function of a deprivation operation for a different reinforcer (food). While FR size adjusted to and total number of bar-presses emitted per session replicate across subjects, other measures (IRI, PRP and wheel turns) are not as reliable.

For example, with regard to PRP, a systematic relationship between length of PRP and deprivation condition was obtained for only three of eight subjects. The PRP value obtained at the 100% end point was greater than at least one of the other deprivation points for all subjects except Subject 8. Overall, these findings are surprisingly consistent as systematic PRP data have been typically observed only when steady-state behavior is obtained (Felton and Lyon, 1966). In Felton and Lyon's (1966) study, pigeons key-pecked on several FR schedules and were stabilized at each FR value.

The present study used an incrementing FR schedule (within sessions) which prevented development of stable responding. Informal observation of the animal's performance suggested there was generally no relationship between the first response which defined the PRP and the remaining number of responses. Regardless of FR size, responses tended to occur in "bursts" rather than the typical "break-and-run"

pattern (Millenson and Leslie, 1979).

The IRI data were similar to the PRP results in that a systematic relationship between length of IRI and deprivation was obtained for only three of eight subjects. With the exception of Subject 8, the IRI value obtained under free food conditions was greater than at least one of the other deprivation points for all subjects. These findings, together with the PRP data, suggest that food deprivation affects the reinforcing efficacy of wheel running. However, the lack of a consistent relationship between deprivation conditions and PRP or IRI data suggests that these measures are not sensitive indicators of the reinforcing value of wheel running.

The wheel turns emitted per opportunity variable did not reveal a more consistent relationship with deprivation conditions than the PRP or IRI data. However, an examination of the wheel turns results raises several interesting issues. First, these data suggest that the reinforcing value of a stimulus is not necessarily equal to its consumption. To illustrate, for Subjects 2 and 5 amount of wheel turns per opportunity did not differ between the 100% and 75% conditions even though substantially more bar-pressing was observed under the 75% condition. Another interesting finding was that over all deprivation conditions female subjects generally exhibited a greater amount of wheel turns than male subjects. This discrepancy may be explainable by male-female differences in body weight. Alternatively, the

data may reflect a sex based difference in activity level. None the less, further research should attempt to control for body weight differences between male and female subjects. Finally, from a methodological standpoint it is interesting to note the large number of wheel turns performed by all subjects. It is possible that when differences in number of wheel turns across conditions were not obtained (e.g., Ss 2 and 5 under the 75% and 100% conditions) this may be due to a "ceiling effect". This might occur because of the 60-sec opportunity to run combined with a high operant level for running by these animals. However, even with the possibility of a ceiling effect on amount of wheel running, it is notable that more bar-pressing occurred under the 75% deprivation condition for Subjects 2 and 5 than under free food conditions, again suggesting that reinforcing value is not equal to consumption.

The inverted U-shaped function relating total number of bar-presses and deprivation level was obtained for all animals (see Figure 1). Interestingly this function, though similar in form, varied considerably from animal to animal. Sidman (1960) has suggested that individual differences among subjects("intrinsic variability"), may lead to variable results upon being exposed to experimental manipulations ("imposed variability"). To try and eliminate such variability, Sidman suggests strengthening the variables which are directly responsible for maintaining the

behavior, bar-pressing in the present case. For example, increasing Ss levels of food deprivation and increasing the amount of time for wheel-running (enlarging the size of reinforcement). In general, Sidman has suggested that variability in results may be greatly reduced if one were to "make use of as many as possible of those variables and combinations of variables which are known to exercise a high degree of behavioral control" (p. 165). Thus it is possible that tighter control of Ss age, number of days between sessions, base rates of free-wheel running, and combinations of other possible experimental variables may lead to less variable data.

Another interesting observation from the data is that although higher deprivation levels produced increases in bar-pressing, there is a drop in pressing sustained prior to, or at, the highest deprivation point for all subjects. From activity-deprivation studies (e.g., Duda and Bolles, 1963; Finger, 1951, 1965) it was expected that increases in food deprivation levels would lead to increases in bar-pressing (i.e., the opportunity to run would increase in value). However, only at specific values does bar-pressing increase with deprivation while declining at others, varying from animal to animal (e.g., Figure 1, Subject 1 and 4). This finding also relates to Sidman's (1960) discussion regarding the possibility that intrinsic variability may lead to variable data upon exposure to experimental manipulations.

The present study has implications of theoretical importance which are suggested by the relationship between total number of bar-presses emitted per session and level of food deprivation. The general nature of these data relate to the stimulus conditions under which a particular type of reinforcement supports behavior. Premack's (1962) formulation of the relative nature of reinforcement addresses the relationship between two operants when the more probable one is made contingent on performance of the other. However, this model does not deal with the findings of the present study. That is, Premack's analysis does not reveal the "establishing operations" (Michael, 1982) necessary for generating a high frequency behavior. [2] The relationship found between bar-presses and food deprivation may be understood from this perspective. That is, food deprivation appears to be an establishing operation that increases the "value" of wheel running as a reinforcer. However, it should be noted that the more typical analysis stipulates that in order to increase (or "establish") the effectiveness of a reinforcing stimulus it is necessary to deprive the organism <u>of that same stimulus</u>.

Further research would be informative as to the generality of the present findings. For example, a study

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[2]Michael (1982) has suggested the use of the term "establishing operation" for operations such as deprivation which have the following two distinct effects on behavior. One effect is to cause an increase in the effectiveness of some stimulus object or event as reinforcement. The other is an increase in the frequency of all behavior that has been reinforced by that object or event.

which manipulated activity level and tested for value of food reinforcement would be valuable. Such a study would be helpful in extending the present analysis of the relationship between these two stimulus events.

In conclusion, at present there are no clear principles pertaining to the effects of deprivation for one stimulus object or event affecting the reinforcing efficacy of another. The present study has demonstrated that a deprivation operation for a stimulus (food) can have an effect on the value of other stimulus events (such as running in an activity wheel). Thus, it is possible that deprivation manipulations as motivational operations may have a more global effect on the organism than is presently suspected. In addition, if the present type of relationship is found across different types of reinforcing stimuli, then the concept of "establishing operations" will have to be broadened. Finally, the possibility of this type of relationship being general across different types of reinforcement has practical and theoretical implications. For example, similar relationships may affect the prediction and control of behavior in applied and basic settings. Further research is required in order to investigate such relationships.

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VI. APPENDIX A: LITERATURE REVIEW

The operant principle of deprivation is that of an operation of withholding access to a stimulus which then affects the reinforcing value of that same stimulus (Skinner, 1938). However, the results of the present study suggest that deprivation for food can affect the value of wheel running. The possibility of a relationship between the reinforcing efficacy of one stimulus and deprivation for another was implied by findings of three related areas of literature. First, the activity-deprivation literature has revealed that certain species of rodents will increase activity as measured by wheel running when they are food deprived (e.g., Finger, 1951). Second, Premack's (1962, 1965, 1971) work concerning the relative nature of reinforcement, has shown that a less frequent response (e.g., bar-pressing) may be reinforced by the opportunity to perform a more frequent response (e.g., running in an activity wheel). Finally, studies have shown that wheel running is effective reinforcement for bar-pressing (Kagan and Berkun, 1954). The purpose of the present review is to examine studies relating activity and deprivation for food, water or both of these stimuli. Also, to briefly review evidence of the reinforcing efficacy of wheel running. In addition, of major interest is the theoretical consideration of food deprivation as an "establishing operation" (Michael, 1982). The final section of this literature review deals with possible proximal and distal interpretations of why

wheel running activity increases with deprivation.

A. Activity and Deprivation

In the activity-deprivation literature there are many studies which have demonstrated that certain species of rodents will substantially increase wheel running when they are food deprived. For example, Finger (1951) using rats investigated the effects of two levels of food deprivation (24 and 72 hours) upon activity. He found that amount of running wheel activity increased markedly with deprivation level. In a later study, Finger (1965) replicated this effect using three levels of food deprivation (0, 24 and 48 hours).

In another experiment, Hall and Hanford (1954) also found that rats on 23 hour food deprivation showed a marked increase in daily running activity compared to control animals which were on free food. Weasner, Finger and Reid (1960) found that rats on a 23 hour deprivation schedule housed in activity wheels failed to maintain stable weight. Routtenberg and Kuznesof (1967) extended the findings of Hall and Hanford (1954) and Weasner et al. (1960) to examine the extent to which activity wheel behavior of rats on food deprivation leads to failure to maintain body weight. These authors investigated "self-starvation" of rats housed in activity wheels and maintained on a 23 hour deprivation schedule. [3]

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[3]Routtenberg and Kuznesof (1967) used the term "self-starvation" to depict the reciprocal nature of the

Routtenberg and Kuznesof (1967) found that rats which were kept on 23 hour food deprivation and allowed free access to a running wheel self-starved and died. These animals showed a significant increase in activity (in terms of wheel turns) over days. However, these animals also revealed a marked decrease in food ingestion as compared to control subjects. Control subjects on the same deprivation schedule but not given access to a running wheel managed to stabilize body weight and survive.

In terms of the present study, certain features of Routtenberg and Kuznesof's (1967) experiment are interesting. First, their findings support the general case that activity increases with deprivation. More interesting is the drop in food ingestion found in deprived animals as compared to controls concomitant with increasing activity levels as deprivation for food increased. This suggests that activity was increasing in reinforcing value as compared to the value of food. The results of the present study are supportive of this interpretation. In addition, the present research attempted to measure (via PRP, total number of bar-presses, etc.) how the value of wheel running increases with food deprivation.

Further evidence demonstrating that activity affects food intake was presented by Levitsky (1974). In this study it was found that access to a running wheel significantly

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[3](cont'd)high increase in activity concomittant with marked decrease in food consumption observed in their experimental animals.

disrupted rats normal meal frequency by reducing the number of meals consumed per day. Food intake was severely depressed for the active animals for the first 4 to 6 days following introduction of the wheel.

In another experiment, Cornish and Mrosovsky (1965) investigated the effects of food deprivation upon activity in six species of rodents. It was found that after 3 days of total deprivation rats and guinea pigs (non-hibernators) increased wheel running; whereas dormice, ground squirrels and chipmunks (hibernators) showed no change (or actually declined in the case of chipmunks) in wheel running activity. The only exception was the hamster (a hibernator) which increased activity with deprivation, presumably because of its reliance on hoarded supplies of food during the winter. In addition to Cornish and Mrosovsky's (1965) study, adding to the generality of this phenomenon, Stefan (1980) found an increase in wheel running with food deprivation in both rats and mice.

Campbell (1964) using rats separately examined the effects of water and food deprivation upon activity measured in stabilimeter cages and activity wheels. He found no appreciable increment in activity with water deprivation using the stabilimeter cages, as compared to "sizeable" increments in activity by food-deprived animals. This sharply contrasts the activity wheel measures obtained in the latter half of the study. In this section it was found that both food and water-deprived rats showed rapid and

substantial increments in activity during the course of deprivation. Campbell (1964) cited two observations regarding these differential results. First, it was found that rate of weight loss was higher in activity wheels than in stabilimeter cages at all temperatures used for both water and food deprivation. [4] Secondly, it was found that survival time is much longer for rats housed in stabilimeter cages than for rats housed in running wheels. In terms of the reinforcement value of random activity in stabilimeter cages versus running in an activity wheel, Campbell's study suggests that the latter activity has greater reinforcement value during deprivation.

Finally, certain studies have analyzed the effects of combined food and water deprivation upon activity. For example, Wright, Gescheider and Johnson (1966) using rats examined the effects of 72 hour continuous food and water deprivation upon wheel running. It was found that activity increased as a function of deprivation for these stimuli.

In conclusion, studies have shown that certain species of rodents will significantly increase wheel running when they are food deprived. In addition, studies have indicated that rats will increase activity (wheel running) when food- or water-deprived, or deprived of both extending the generality of the activity-deprivation phenomenon.

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[4]Campbell (1964) used several temperatures as he was interested in "the nature of the metabolic and regulatory processes that govern rate of weight loss, terminal weight loss, and survival time of food and water-deprived rats as a function of environmental temperature in both wheels and stabilimeters"(p. 325).

B. The Reinforcement Value of Wheel Running

Evidence that running in an activity wheel can be used to reinforce instrumental behavior, such as bar-pressing, comes from studies by Kagan and Berkun (1954) and Premack (1962).

Kagan and Berkun's (1954) study used two groups of free-feeding rats to determine if the opportunity to run in an activity wheel is adequate reinforcement for bar-pressing. Initially, one group received 30 seconds of free-wheel time for a single bar press, while bar-pressing by a control group was ineffectual in obtaining free-wheel time. The controls were yoked to the test subjects and received free-wheel time when the test Ss did. The test animals pressed somewhat more during this phase of the experiment. The rats were then put on a fixed-interval schedule during which 30 seconds of free-wheel time was given only for the first response to occur after 0, 2.5, 5, 7.5 and 10 minutes from the beginning of the session. Both groups pressed the bar at a higher rate than during the former phase. The experimental animals, however, pressed at almost three times the rate of the controls. Therefore, Kagan and Berkun (1954) concluded that bar-pressing can be reinforced by the opportunity to run in an activity wheel.

Premack's (1962) study also indicated that the opportunity to run in a wheel can be used to reinforce instrumental behavior. In part of this study, a fixed ratio of five licks from a retractable drinkometer while the wheel

was locked released the braked wheel for 10 seconds of free-wheel time. It was found that with running contingent upon drinking, total drinking was increased in all rats by a factor of three to five. The results showed that for operant level drinking, with only the drinkometer tube present, mean total drinking time was about 28 sec/hr; both tube and wheel present decreased this time to 23 sec/hr; and with running contingent upon drinking, total drinking was an average of 98 sec/hr.

In summary, both of these studies showed that rats will press a bar or engage in other instrumental behavior (such as drinking from a retractable tube) in order to run in an activity wheel. That is, wheel running can act as reinforcement for other operant behaviors.

C. Food Deprivation as an Establishing Operation

According to Michael's (1982) recent paper, food deprivation may be seen as an "establishing operation" (EO). By definition an EO is "any change in the environment which alters the effectiveness of some object or event as reinforcement and simultaneously alters the momentary frequency of the behavior that has been followed by that reinforcement"(Pp. 150-151). The behavioral effects of food deprivation may be stated in these terms. The first effect of food deprivation is an increase in the effectiveness of food as reinforcement for any new behavior which happens to be followed by access to food. The second effect is to

increase in frequency all behavior that has been reinforced with food.[5] Therefore, if an increase in wheel running during food deprivation happens to lead to food reinforcement, then running would be expected to increase in frequency upon subsequent deprivation periods.

Michael's (1982) analysis of the behavioral effects of deprivation has determined that operant behavior can be evoked or increased in frequency in two different ways. Michael gives the following example for consideration: an organism is at least somewhat water-deprived and has a history of water reinforcement for some class of responses; the current stimulus conditions have been associated with a low, but non-zero, frequency of water reinforcement for those responses. These responses "can be made momentarily more frequent (1) by further depriving the organism of water, or (2) by changing to a situation where they (the responses) have been more frequently followed by water reinforcement (the discriminative stimulus effect)"(p. 150). Michael suggested the use of the term "establishing operation" for operations having these effects on behavior.

The effect of food deprivation in the present study appears somewhat different than the effects suggested by Michael (1982). Michael's analysis of food deprivation as an EO does not describe the effect found in the present study that food deprivation had upon the reinforcing efficacy of <u>another</u> stimulus event (running in an activity wheel). It

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[5](Note that the latter effect is equivalent to the evocative effect of a discriminative stimulus.)

appears that the first effect of stimulus deprivation as an EO as previously stated results in changes in reinforcing value of <u>that stimulus only</u>. The present research suggests an addendum to Michael's two behavioral effects of deprivation. This addendum would suggest that deprivation for one stimulus object or event may have an effect upon the value of <u>other</u> stimulus objects or events. The inclusion of this effect of deprivation would enlarge the scope of the concept of establishing operations. Thus, establishing operations would be able to describe deprivation operations affecting one stimulus only, as well as the effects of deprivation for one stimulus on the reinforcing value of another as in the present study. Such a broadened concept of EO may be helpful in elucidating further the effects of deprivation.

D. Proximal and Distal Explanations

Proximal and distal explanations of why wheel running increases with food deprivation reveal different viewpoints regarding this phenomenon. Proximal explanations could, for example, appeal to immediate physiological parameters such as the relationship between hypothalamic activity and locomotor activity (Routtenberg and Kuznesof, 1967), or the relationship between locomotor activity and temperature regulation (Stevenson and Rixon, 1957; Campbell, 1964). Distal explanations, on the other hand, could appeal to evolutionary or phylogenic processes regarding individual or

species survival (e.g., having to re-locate, by increasing activity, to find food) as discussed by Skinner (1966, 1975).

Routtenberg and Kuznesof's (1967) research provides an example of a proximal explanation. These authors hypothesized, first, that food deprivation causes "hunger" and weight loss, which lead to overactivity in specific lateral and posterior hypothalamic nuclear systems. Second, hypothalamic activity along with locomotor activity produce certain physiological "products" which somehow act as signals of food to the hypothalamus, thus depressing food intake. Routtenberg and Kuznesof's (1967) hypotheses clearly appeal to a proximal physiological explanation of why rats run in response to food deprivation, plus why activity reduces food intake.

Another proximal explanation which appeals to physiological parameters is that of the temperature regulation hypothesis suggested by Stevenson and Rixon (1957) and later by Campbell (1964). Stevenson and Rixon (1957), for example, concluded that the increase in activity during food deprivation is related to the maintenance of body temperature. These authors suggested that the normal physiological response to food deprivation is a fall in body temperature, which then "motivates" an increase in the rat's activity level which eventually restores normal body temperature. In support of this, measurements taken of body temperature indicated that temperature decreased during

starvation when activity was restricted, but not when permitted.

Distal explanations, in sharp contrast to proximal explanations, are not concerned with possible immediate reasons for changes in behavior. Increases in activity during food deprivation would not be thought of as being important in raising body temperature, unless this increase in temperature had long-term benefits for the individual and ultimately, the species.

In this regard, Skinner (1966, 1975) has written at length regarding the similarities between the shaping of phylogenic and ontogenic behavior. Phylogenic behaviors are inferred to be due to contingencies of survival, i.e., to be of evolutionary value. Thus, the increase in activity during deprivation may be thought of as a phylogenic behavior pattern which was shaped much like ontogenic behavior studied in the laboratory. For example, the organism which foraged outside of its territory when food supplies became scarce, and found food by doing this, would tend to repeat this successful behavior pattern the next time food was scarce. Such an increase in foraging during food shortages is of obvious survival value and it is probable that such behavior would be strengthened by genetic selection and operant conditioning. That is, the organisms which survive during food shortages in the above example would be the organisms whose foraging behavior could be strengthened as contingencies change (e.g., as food shortages become more

severe requiring more foraging), thus allowing reproduction and species survival. In other words, when the shaping of an effective behavior is strengthened by selection of genotypes there is an increase, according to Skinner (1975), in "the probability that behavior having a given topography and under the control of given stimuli will actually occur"(p. 120). Such explanations of behavior are of an obvious distal nature.

In conclusion, proximal and distal explanations regarding the increase in activity observed during food deprivation appear widely divergent. However, Skinner (1975) in outlining the similarities between phylogenic and ontogenic behavior noted that we do not know whether the physiological changes associated with the shaping of these types of behavior are similar. Skinner (1975) suggested that it is not impossible that ontogenic behavior and its conditioning as "an evolved feature of the organism, should have utilized a physiological system that had already been developed in natural selection"(p. 120). Thus, the shaping of ontogenic and phylogenic behavior could possibly be closely related. If this were the case, proximal vs. distal explanation (e.g., physiology, ontogeny vs. phylogeny) would become different, but related, levels of analyses of common phenomena, rather than elucidating what presently appears to be entirely different areas of study. Such a "levels of analyses" approach would integrate physiological theories of food deprivation and activity with ontogenic and phylogenic

explanations of such phenomena for a more thorough and comprehensive analysis.

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